

## Ecology of the woodwasp *Sirex noctilio*: Tackling the challenge of successful pest management

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The invasive woodwasp *Sirex noctilio* has become one of the most significant pests of pine forests throughout the northern and southern hemispheres. In Patagonia (southern Argentina), *S. noctilio* was first detected in the early 1990s. However, in less than two decades, and despite intensive control efforts, populations have spread, and outbreaks have been observed. In this paper, we outline and define several key ecological and behavioral features of *S. noctilio* (namely, spatiotemporal population dynamics, phenology and dispersal) and briefly discuss their implications for the design, implementation and evaluation of local and regional management strategies. We argue that limited information on pest ecology and the extrapolation of control measures without local adaptation may together have affected management success. We conclude that efforts directed to understanding of pest ecology and life-history traits as expressed in specific invaded habitats may help us improve our competence in controlling invasive forest insects.

**Keywords:** forest pests; integrated pest management; invasive insects; population ecology; woodwasp

### 1. Introduction

The quest for ecological knowledge of alien insects lies at the core of most forest pest management plans (Sakai et al. 2001; Liebhold and Tobin 2008; Slippers and Wingfield 2012). Non-native forest insects are among the most damaging threats to forest resources in the world; their impact may be even stronger than that of other disturbances such as fires or storms. Since transport pathways have increased markedly over the past centuries, mainly due to the globalization of trade, propagule pressure – that is, the number of individuals arriving at a site and the number of dispersal events – has promoted an exponential increase in arrival rates of alien insect species in forests (Lockwood et al. 2007; Liebhold and McCullough 2011; Liebhold et al. 2012). Luckily, only a fraction of these species manages to establish, spread and cause substantial impacts to forest ecosystems. Understanding the life-histories and ecology of the successful invaders can not only help prevent future invasions, but also improve our abilities to manage already established and spreading populations.

The woodwasp, *Sirex noctilio* Fab. (Hymenoptera: Siricidae), exploits many pine species, including commercial trees planted throughout the northern and southern hemispheres. Native to Eurasia and North Africa, *S. noctilio* has invaded several other regions of the world such as Australasia (Madden 1988), South America (Iede et al. 1998), South Africa (Tribe 1995) and more recently, North America (Hoebeker et al.

2005). Partly because *S. noctilio* is an invasive insect, it has become one of the most economically significant pests of softwood forestry in most invaded areas and a serious threat to local forests in regions where pines are native (Madden 1988; Hurley et al. 2007).

*Sirex noctilio* was originally detected in Argentina in 1985 (Espinoza et al. 1986). However in Patagonia, a region located in the south of the country, the first detection of this wasp occurred in the early 1990s, in infected wood at a lumber yard, near to the city of Bariloche (41°04'S, 71°10'W; Aguilar et al. 1990). In subsequent years, attacked trees were detected in *Pinus radiata* stands, located close to the arrival site (Klasmer et al. 1998). In less than two decades since its detection, and despite limited control efforts, *S. noctilio* has spread throughout the region. At a regional scale, populations of *S. noctilio* remain generally below endemic population levels, but severely damaging outbreaks have been observed at several sites (Villacide et al. 2009; J.M. Villacide and Corley, unpublished data).

Management of *S. noctilio* populations in southern Patagonia as well as in other regions invaded by this pest has been based on protocols developed predominantly in Australia and New Zealand. A notable point here is that, in general, management strategies for this forest pest have been applied without proper validation or local adaptation to the environmental and productive scenarios of the new sites (Slippers and Wingfield 2012). The variable success obtained worldwide using

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biological control involving the entomopathogenic nematode *Beddingia* (= *Deladenus*) *siricidicola* – a cornerstone of most management strategies developed for *S. noctilio* – probably illustrates this problem most clearly (Hurley et al. 2007, 2008).

In line with the implementation of control measures in several invaded regions, considerable research has been carried out during the last decades, leading to an improved understanding of the general biology of *S. noctilio*. Several aspects of the wasp's chemical ecology, interaction with host trees and the fungal symbiont *Amylostereum areolatum* have been extensively studied (for a recent global compilation, see Slippers et al. 2012). However, little is yet known about the behavioural and population ecological factors that may have promoted invasion success, even under very diverse environmental conditions and forest management practices (e.g. Southern Argentina and South Africa; Corley and Villacide 2012; Slippers and Wingfield 2012). As a consequence of this and despite that *S. noctilio* is widely recognized as an invasive species (Carnegie et al. 2006; Hurley et al. 2007; Yemshanov et al. 2009; Dodds et al. 2010; Corley and Villacide 2012), ecological processes involved during the course of the invasion are rarely considered in the design, implementation and evaluation of local and regional management strategies.

In this paper, we define and describe several key ecological and behavioral features of *S. noctilio* in Patagonia and discuss their implications on population management. We set our emphasis on those aspects of the biology of the species that explain invasion success, illustrating how this knowledge may help understand past failures and successes in woodwasp population management. This may help increase our capabilities in controlling this and other invasive forest insects.

## 2. Outbreaks and spatial ecology of *Sirex noctilio* populations

The most significant ecological feature of *S. noctilio* is the occurrence of a pulse-like pattern of eruptive population dynamics (Madden 1988; Corley and Villacide 2012). Eruptive dynamics are characterized by long time periods during which the populations remain at relatively low densities but may rapidly increase to outbreak levels (Berryman 1987). It is during these population outbreaks that *S. noctilio* may cause extensive tree mortality, even to healthy and vigorous trees.

Although severe damage and tree mortality are easily visualized in the field, quantitatively defining endemic and epidemic levels and outbreak thresholds and the mechanisms leading to outbreaks are still unclear. It is important not only to allow for comparisons between sites and regions, but also to clearly establish the type and degree of management intervention procedures. Based on experimental and

field experience, we propose here a rule of thumb to define population stages (for specific details refer to Bruzzone et al. 2005; Villacide and Corley 2006; Corley et al. 2007; Corley and Villacide 2008). We consider that the pattern of population growth of *S. noctilio* can be viewed as a continuum, in which different stages may be identified (Figure 1).

At initial colonization stages (endemic levels), *S. noctilio* populations are typically small and, therefore, the proportion of attacked trees does not exceed 1% of the available trees in a given stand. At this stage, woodwasp female attacks are concentrated among stressed trees as a product of intra-specific competition and/or other stressing factors such as droughts, fire or physical damage.

At a second stage, which may be associated with large-scale climatic events, among other generalized tree-stressing events, a pre-outbreak scenario is established, during which attack rates increase to values above 1% and up to 5% of trees in the stand. During such pre-outbreak conditions, female wasps select a wider range of tree conditions for attack, including dominant and more vigorous trees. Also, at this stage, spatial aggregation becomes stronger (Corley et al. 2007). Finally, the onset of an outbreak may be defined as when populations reach 5% of attacked trees (Aparicio et al. 2012). These abundance peaks commence at spatially local foci and quickly expand to cover larger areas in one or a few seasons. Aggregation patterns during this stage become less visible due to the more widespread attacks. Outbreak duration is variable, between 1 and 10 years, and can reach damage levels of up to 80% of all trees within a stand (Madden 1975, 1988; Haugen 1990; Villacide et al. 2009). After the outbreak, *S. noctilio* populations decrease due to the action of natural enemies, adult emigration and/or resource limitation (Berryman 1986).

Two main mechanisms have been proposed to explain the observed population dynamic patterns of *S. noctilio*. Madden (1988) suggested that density-independent factors such as fire, inappropriate silvicultural practices, windstorms or drought periods can promote the onset of the epidemic stages. Here, the occurrence of these factors during or between the adult emergence seasons can lead to physiological changes in host trees, which consequently increase their attractiveness and susceptibility to wasp attacks. The attraction of wasps towards suitable trees is known to be primarily via responses to volatiles (typically  $\alpha$ - and  $\beta$ -pinene) released from bark tissue (Madden 1968; Crook et al. 2012).

Alternatively, Corley et al. (2007) have proposed that population outbreaks are closely related to strong spatial aggregation of attacked trees, as a consequence of limited female wasp spatial re-distribution. Spatial aggregation of *Sirex*-infected trees is important even during early establishment stages (endemic phases) and even increases as attack rates increase (Corley et al.

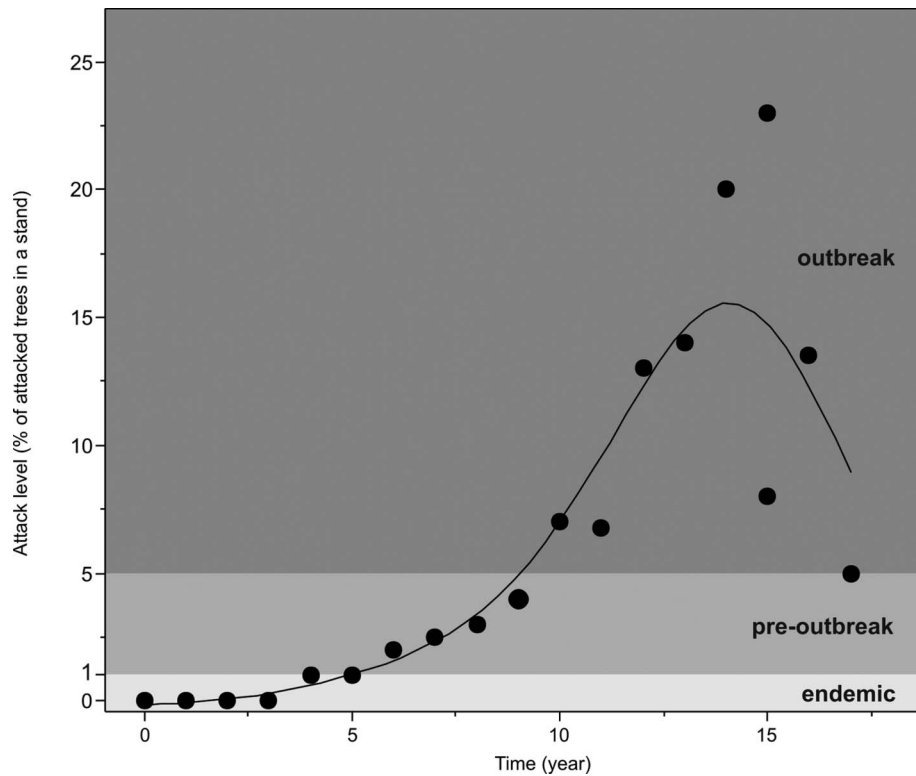


Figure 1. General pattern of *Sirex noctilio* population growth (extracted from Madden 1968). Given the pulse-like outbreak dynamics, population growth can be viewed as a series of stages, determined by population sizes or tree mortality intensity. Here, based on ecological mechanisms and life history traits of *S. noctilio*, we define endemic and epidemic levels and outbreak thresholds. Endemic populations (lighter grey) are visible when attack rates are under 1% of trees in a stand. Pre-outbreak conditions (intermediate grey) occur when attacked trees found are between 1% and 5% of all trees. Finally, outbreaks are defined by attack rates exceeding 5% of the trees in the stand (darker grey).

2007). Due to strong spatial aggregation, healthy and vigorous trees (i.e. dominant trees) can be overwhelmed through repeated inoculations of fungal spores and phytotoxic mucus (Madden 1968, 1974; Figure 2). The trees are killed by the combined effect of the symbiotic fungus inoculated by females for the larvae to feed on and mucus that affects tree normal physiology, supporting fungal and wasp larval development (Coutts 1968; Coutts and Dolezal 1965, 1969).

Knowledge of the factors explaining outbreaks and spatiotemporal patterns of populations in invaded areas remains central to *S. noctilio* management. This is because understanding the relative roles of density-independent and density-dependent factors and establishing threshold populations are critical to predicting epidemics and establishing alarm systems. Note that economic losses are minimal during endemic population phases and that some intervention practices such as sanitary thinning are feasible during these stages only. This major research topic deserves still further, specific work, where it is likely that modelling will take a lead. In turn, the spatial pattern of *S. noctilio* attacks may preclude the application of population sampling techniques. For instance, sequential sampling protocols, as that developed by Penteadó et al. (1998, 2002) is a practical and low-cost method widely used in South

America, The method, however, assumes a random spatial distribution of wasp attacks within a stand, which may only be true during outbreak phases (Corley et al. 2007; Aparicio et al. 2012).

### 3. Invasion ecology: what factors contribute to the observed spread?

Currently, *S. noctilio* populations are established in most pine plantations of southern Argentina (Corley et al. unpublished data). Globally, invasion of *S. noctilio* into new areas has been strongly associated with the accidental introduction of infested wood materials. For example, transport of immature stages via solid wood packaging or infested timber is presumed to be one of the main pathways by which *S. noctilio* has dispersed among distant regions. However, at a regional scale, both establishment and spread success can also be explained by several life-history traits of *S. noctilio* (Villacide et al. 2010, 2011; Corley and Villacide 2012).

Spread of *S. noctilio* populations in Patagonia since their arrival in 1993 remained largely static until the year 2000. Since then, until 2006, a significant increase in spread rates has been observed (Corley et al. unpublished data). In the last two decades, north-western Patagonia was importantly affected by a higher

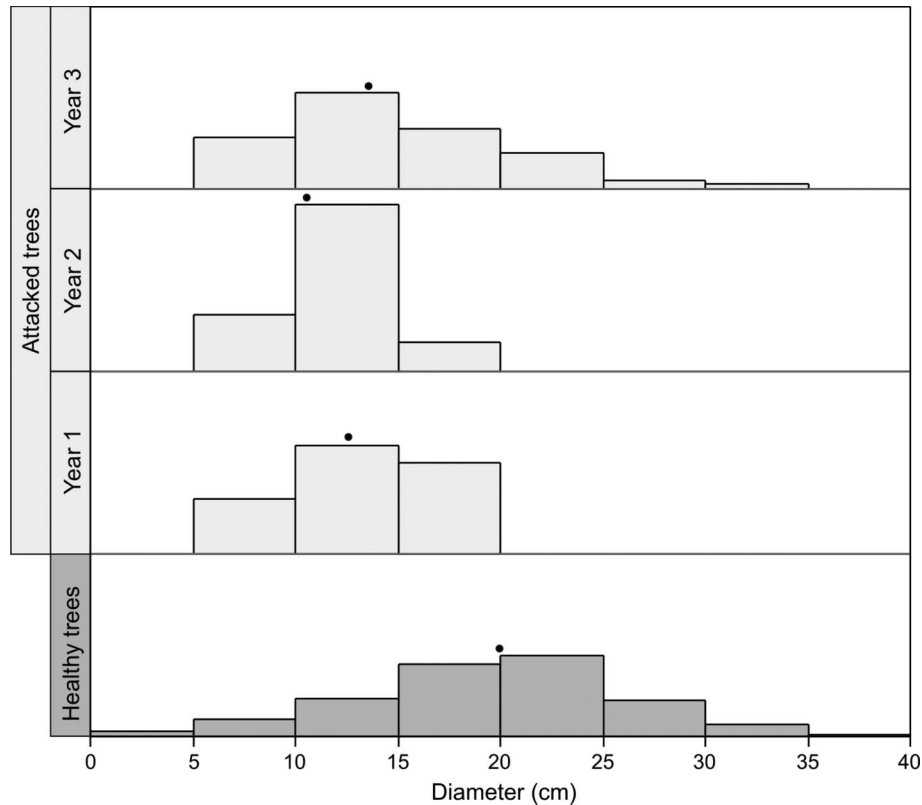


Figure 2. Frequency distribution of tree diameter (dbh; diameter at breast height in cm) in a recently *Sirex*-invaded pine stand. The upper panels show the frequency of the dbh of infested trees over the 3 years since first detection of *Sirex noctilio* in the stand, obtained through a tree census. The lower panel shows diameter distribution of healthy trees, determined through a forest inventory. Black circles indicate mean dbh (modified from Villacide and Corley 2006; Villacide and Corley unpublished data). Note that as consequence of spatial aggregation and population growth (Villacide and Corley 2006, Corley et al. 2007) female wasps progressively select larger trees.

frequency of drought periods (i.e. 10 severe drought events, in contrast to only 6 droughts recorded in the previous 80 years; Mundo et al. 2010), presumably related to ENSO (El Niño Southern Oscillation) phenomena (Fundación Torcuato di Tella 2006; IPCC 2007). For instance, an intense drought was recorded during a four-year period (1995–1999) with precipitation levels significantly below the regional climatic historical records (data from National Weather Service of Argentina). It is possible that such conditions have generated a greater availability of stressed pine trees, as these are mostly grown in dry, steppe areas (Fernandez et al. 2012). After this, resident *S. noctilio* populations increased and some moderate-sized outbreaks were observed (Villacide, unpublished data), which may have led to increased propagule pressure and the observed incremental spread and widespread distribution of *S. noctilio* populations in the region.

Despite a highly fragmented landscape in Patagonia – pines there are typically cultivated in patches of variable size in a steppe vegetation matrix – *S. noctilio* populations have spread at an average rate of 17.7 km/year (Corley and Villacide 2009; Corley et al. unpublished data). This spread rate is slower than that

observed for other regions in the southern hemisphere. For example, spread rate in South Africa is estimated for a 9-year period (1993–2002) to be approximately 47 km/year whilst that in Australia (South Wales) during 1980–2002 period, such rate is close to 40.1 km/year (J.C. Corley, Villacide and Liebhold, unpublished data).

Several factors could influence the spread rate of *S. noctilio* and promote the differences observed between Patagonia and other invaded regions. Environmental factors such as climate, the degree of landscape fragmentation as well as reported differences in silvicultural management and in the efficacy of control strategies are important aspects. However, because spread rate is basically determined by the combined action of population growth and dispersal (Shigesada and Kawasaki 1997; Lockwood et al. 2007), life-history traits of *S. noctilio* can also play a role in explaining the observed geographical spread. For instance, local population density and population dynamics patterns as well as the occurrence and/or fraction of the population delaying adult emergence (Corley 2001; Corley et al. 2004; Corley and Villacide 2012) not only may determine the local abundance of wasps but also their individual characteristics such as

egg loading, body size (i.e. flight capacity, longevity) and dispersal behavior.

Adults of *S. noctilio* are remarkably capable flyers. Using flight mill devices, Bruzzone et al. (2009) have shown that the potential distance flown by females could range from 1 km to 50 km in one day. Reported variability in flight is related to body size: while larger females can carry out long (more than 6 hours), sustained flights over long distances, smaller females fly much less and stop repeatedly. *S. noctilio* males, in turn, have shown a lower flight ability than females, with distances between 1.6 km and 30.3 km/day (Villacide and Corley 2008; Corley and Villacide 2012).

Strong dispersal behaviour has also been observed in field conditions, even when local populations are at endemic levels (Villacide and Corley, unpublished data). Adult trapping (with  $\alpha$ - and  $\beta$ -pinene baited interception traps) in a non-pine habitat at several distances from Sirex-infested plots, showed that at distances up to 4000 m from the plantation edge, mated female woodwasps were captured (Villacide and Corley unpublished data). The observed dispersal pattern, coupled with a known mating behaviour (i.e. mating occurs before dispersal) and a single-locus sex determination system may help mitigate potential Allee effects occurring in new, incipient populations (Liebhold and Tobin 2008; Kramer et al. 2009).

Prolonged diapause, a life-history feature of many insects, which facilitates temporal synchrony with unpredictable variations in habitat (Tauber et al. 1986; Danks 1987), has also been observed in *S. noctilio* populations in cool-temperate climates (Corley et al. 2004). In Patagonia, prolonged diapause affects a considerable fraction of the *S. noctilio* population: approximately 75% of adults emerge during the first year since oviposition; close to 24% in a second year and the rest of the progeny emerges during a third year (Corley 2001).

Prolonged diapause can also have an important role in determining the population dynamics of *S. noctilio* (Corley 2001). Consider two populations with similar size and identical growth rates, but that vary only in displaying extended diapause: the intensity and/or duration of epidemic outbreaks in the population with delayed emergence will be lower than that one lacking such phenology (Corley and Villacide 2012). In addition, insects diapausing for long periods inside wood or timber increase the chances of accidental transportation into new areas. Finally, at an individual scale, prolonged diapause can lead to variations in adult body size because they may relate to differential availability of food resources for developing larvae (Morgan 1968; Corley and Villacide 2012; Ryan and Hurley 2012). Since attributes such as flight capability, survival rate, longevity and potential fecundity are closely correlated with adult size, the effects of prolonged diapause on population dynamics and their

implications in invasion success are matters that require more detailed studies (Mahdjoub and Menu 2008).

#### 4. Concluding remarks

A critical review of the results obtained in the control of *S. noctilio* populations in southern Argentina, in the light of knowledge on the ecology and behaviour of the pest may help us understand the reasons behind its variable success and improve future measures. Despite a major investment in a set of control actions carried out since detection in the region, populations have spread and several severe outbreaks have been recorded (Villacide, unpublished data). Several of the control measures were based on limited information on the pest biology in the region, and rarely took into account concepts of invasion ecology. Moreover, such measures were implemented following protocols developed for other regions, and so lacked proper local adaptations and did not always consider differences in forestry practices and conditions (Hurley et al. 2007, 2008; Villacide and Corley 2008; Slippers and Wingfield 2012).

Biological control of *S. noctilio* populations in Patagonia was essentially accomplished through the classical introduction of several natural enemies. The parasitoid wasp *Ibalia leucospoides*, however, was not introduced deliberately into the region, but arrived together with *S. noctilio*, rapidly becoming established throughout the distribution range of the pest (Villacide and Corley 2003). Although this parasitoid is generally reported to be a successful biocontrol agent of woodwasp populations (Berryman 1986; Kidd and Jervis 1996; Cameron 2012; Klasmer and Botto 2012), this may be true only for given populations, inhabiting specific habitat conditions (Taylor 1978). For example, prolonged diapause, as expressed in the cold climate of Patagonia, may limit the suppressive capacity of this cynipoid parasitoid, given the physiological interaction that is established between host and parasitoid (Corley and Bruzzone 2009). In this sense, the parasitoid is unlikely to be effective in suppressing local woodwasp populations by itself. Also, and despite the fact that females of *I. leucospoides* are capable of displaying long-distance flights, maximum dispersal is limited to approximately half of that of *S. noctilio* (Bruzzone et al. 2009; Fischbein et al. 2011). Here, the contribution of *I. leucospoides* in terms of limiting or slowing the spread of their hosts remains unclear.

The entomophagous nematode *Beddingia siricidicola* in turn, is widely recognized as a most effective biological control agent worldwide (Lacey et al. 2001; Bedding and Iede 2005). While the establishment of nematodes in the field is usually successful, and locally populations can grow fast, parasitizing a large number of hosts in few seasons, the results obtained in terms of actual control (i.e. a reduction of local densities of the

host population, preventing outbreaks, or slowing the spread) are less clear (Hurley et al. 2007; Villacide and Corley 2008). Whilst in some cases limited success in nematode effectiveness has been associated with problems during rearing or manipulation protocols (e.g. loss of virulence or incompatibility with their host), other issues have been less studied. For example, Villacide and Corley (2008) showed that nematode-bearing adult wasps (the dispersers of nematodes within the pest population) are smaller and can fly shorter distances than non-infected individuals. Knowledge of this has implications for the design of introduction and augmentation programmes of nematodes, as it may limit their success at a regional scale (Corley and Villacide 2009; Corley et al. unpublished data).

Additional information on the dispersal capacity and the population dynamics of *S. noctilio* may have led to better results in terms of regional planning measures such as when devising sanitary barriers, inspection protocols and local containment procedures or plantation design. Generally, the arrival of many non-native insects into novel areas is driven by the transport of hidden propagules via transport vectors (for *S. noctilio*, fundamentally through immature stages or latent adults in wood packing, firewood or timber); during the establishment and spread phases, population processes –namely reproduction and dispersal – are involved (Liebhold and Tobin 2008). In this sense, *S. noctilio* propagule pressure may increase during outbreaks (the probability of conveying infected transport vectors increases with increasing population size), favoring spread. It remains to be known if natural dispersal is a density-dependent process and what its contribution is to observed spread. In contrast, the degree of landscape fragmentation (and plantation design) relative to flight potential of adult females could limit spread. Likewise, population mechanisms operating at endemic phases (i.e. Allee effects) and their interaction with the environmental and productive scenario may prove critical to invasion management at a regional scale.

Finally, management of *S. noctilio* populations relies strongly on accurate estimates of pest abundance and careful monitoring, also during endemic populations phases. In this sense, knowledge of the spatio-temporal dynamics influences the reliability of sampling protocols and consequently the intensity and timing of control measures.

Invasions by non-native insect species are currently recognized as a significantly growing threat to forest resources worldwide (Liebhold et al. 1995; Kenis et al. 2009; Brockerhoff et al. 2010). Several reasons highlight the importance of invasive pests in forestry. Noteworthy is the characteristic of productive plantation forestry systems in some areas, where an unusually extensive time-line is involved from establishment to final harvest (Wainhouse 2005). Also, forestry in many regions implies plantation of exotic tree species at high

crop densities and bearing little genetic diversity. While this environmental scenario may allow increased wood and pulp productivity, it also can lead to an increase of favorable niches for the establishment and spread of invasive insects (Wainhouse 2005; Lockwood et al. 2007; Davis 2009).

Notwithstanding the reported advances in our knowledge on the invasion ecology of several species, an important gap between the theory of invasions and its application to pest management still exists (Liebhold and Tobin 2008). Here, by analyzing the control measures implemented for *S. noctilio* in Patagonia and describing key aspects of the pests' ecology, we have attempted to understand invasion success and management of this damaging forest insect. Clearly, to fully comprehend success and failure in containing populations of the invasive *Sirex* woodwasp in our region and other invaded regions, much research is still needed.

Success in eradicating, containing or slowing the spread of invasive forest insects depends strongly on adequate knowledge of those ecological traits of species relevant to invasion success (i.e. dispersal, population dynamics) in the novel environmental scenarios. It is important to note here that invasive insects and forests display complex and dynamic interactions that may preclude generalized recipes for pest management. This implies that considerable effort is necessary to investigate the ecology of pests in invaded areas, to develop new tactics, as well as to validate those available to the specific conditions occurring in novel habitats.

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